Short-term effects of spring prescribed burning on the understory vegetation of a *Pinus halepensis* forest in Northeastern Spain

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HIGHLIGHTS

- Projected higher fire risk requires promoting forest ecosystems' adaptive capacity.
- Low-to-moderate intensity burning preserved understory composition and diversity.
- Burning may reduce flammable seeder shrubs, thus promoting community's resilience.
- Understory prescribed burning may strongly reduce fuel load and spatial continuity.

GRAPHICAL ABSTRACT
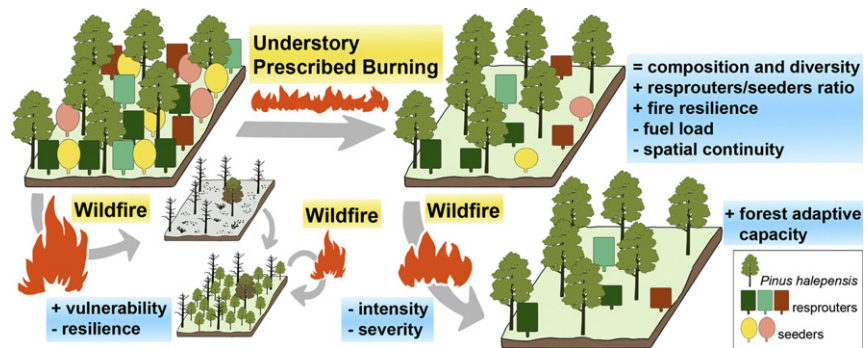
ABSTRACT

Since the 1970s, fire regimes have been modified in the Northern Mediterranean region due to profound landscape changes mostly driven by socioeconomic factors, such as rural abandonment and large-scale plantations. Both fuel accumulation and the increasing vegetation spatial continuity, combined with the expansion of the wildland-urban interface, have enhanced fire risk and the occurrence of large wildfires. This situation will likely worsen under the projected aridity increase resulting from climate change. Higher fire recurrences, in particular, are expected to cause changes in vegetation composition or structure and affect ecosystems' resilience to fire, which may lead to further land degradation. Prescribed burning is a common fuel reduction technique used for fire prevention, but for conservation and restoration purposes as well. It is still poorly accepted in the Mediterranean region since constrained by critical knowledge gaps about, in particular, its effects on the ecosystems (soil, vegetation). We studied the short-term (10 months) effects on the understory vegetation of a spring prescribed burning conducted in a *Pinus halepensis* forest in Mediterranean climate (Northeastern Spain). Our results show that the understory plant community recovered after the burning without short term significant changes in either species richness, diversity, or floristic composition. Most vegetation structural characteristics were modified though. The burning strongly reduced shrub height, shrub and herbaceous percentage covers, and aerial shrub phytomass; especially its living fine fraction, thus resulting in a less flammable community. The treatment proved to be particularly effective for the short term control of *Ulex parviflorus*, a highly flammable seeder species. Moreover, the strong reduction of seeder shrubs frequency in relation to resprouters' likely promoted the resilience to fire of this plant community. From a fuel-oriented perspective, the burning caused a strong reduction of spatial continuity and surface fuel loads, leading to a less fire-prone fuel complex.

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1. Introduction

Fire regimes are variable through time and space, resulting from complex interactions between climate, vegetation characteristics (i.e. type, condition and spatial configuration) and probability of ignition (Pausas and Fernández-Muñoz, 2011; Iglesias et al., 2015).

In the Mediterranean region (MR), anthropic activities have strongly determined during millennia the spatial distribution of vegetation types and land uses in the landscapes, therefore affecting fire occurrence and behavior (Pausas and Keeley, 2009; Moreno et al., 2013). Besides, the human use of fire as a tool for agro-pastoral and forestry purposes influenced fire ignitions and their seasonality (Pausas and Keeley, 2009; Bowman et al., 2011; Iglesias et al., 2015).

In recent decades, agricultural land abandonment (Fernández Ales et al., 1992), large-scale afforestation programs (Vallejo and Alloza, 1998), the prohibition of traditional fire uses and some restrictive fire suppression policies (Castellnou et al., 2010) promoted more homogeneous landscapes characterized by increasing fuel loads and more continuous surface fuels (Moreira et al., 2001; Moreno et al., 2013). Besides, fire ignition probability raised in many landscapes due to the growth of the wildland-urban interface (San-Miguel-Ayanz et al., 2012). An increase of large wildfires has been consequently observed in several northern Mediterranean regions since the 1970's (Loepfe et al., 2010; Moreno et al., 2013), although there is some variability depending on the region and the time period observed (San-Miguel-Ayanz et al., 2012; Koutsias et al., 2013). This tendency is particularly concerning under the current global change context, which is expected to enhance fire risk and shifts in spatial and temporal patterns of fire occurrence in the MR (Moriondo et al., 2006; Moreno et al., 2013). Increased fire recurrences, in particular, could cause changes in vegetation composition or structure and affect ecosystems' resilience to fire (Díaz-Delgado et al., 2002; Eugenio and Lloret, 2004; Espelta et al., 2008). Too short fire-free periods might ultimately cause the local extinction of long-lived woody species and favour herb-dominated systems due to the depletion of the seed banks and/or the decline in soil fertility (Zedler et al., 1983; Keeley et al., 1999; Eugenio et al., 2006). Synergistic interactions between these changes and other ongoing degradation processes mediated by human activities or global warming could finally impair ecosystems' functionality and promote land degradation (Cortina et al., 2009).

Prescribed burning (PB) is a vegetation management technique that is used across the world for controlling fuel load and creating spatial discontinuities in the vegetation (Agee and Skinner, 2005; Marino et al., 2011), and for achieving conservation or restoration objectives as well (Stephens et al., 2014). Various studies conducted in the MR support the interest of applying PB as a fuel management tool to reduce fire risk, limit fire intensity and severity, while improving the ecosystems' resilience to fire (Fernandes and Botelho, 2003; Piñol et al., 2005; Cassagne et al., 2011; Marino et al., 2011; Fernandes et al., 2013; Casals et al., 2016). Its use is still limited to few areas in the MR, though, due to a lack of social acceptance and the remaining uncertainties about its ecological effects, its operational feasibility in a wide range of situations (e.g. risks inherent to fire use when wildland-urban interface is overdeveloped) and its advantages in relation to other techniques (Ascoli and Bovio, 2013; Marino et al., 2014).

Studies assessing the vegetation dynamics after PB in ecosystems of the MR, and particularly those addressing burnings conducted under tree canopies, started quite recently (Vega et al., 1987, 2000; Rego et al., 1991; Moreira et al., 2003; Catalanotti, 2009; Esposito et al., 2014; Casals et al., 2016). In the Iberian Peninsula, to our knowledge, all studies dealing with PB effects on the understory vegetation have been carried out in *Pinus pinaster* Ait. or *Pinus nigra* Arn. ssp. salzmannii (Dunal) Franco stands. The present study is innovative, since conducted in a *Pinus halepensis* Mill. monospecific forest. Such type of woodlands experienced a great expansion in Spain throughout the second half of the XXth century driven by afforestation efforts and colonization after land abandonment (Barbero et al., 1990; Pausas et al., 2008). When dense and monospecific, these forests are often very flammable, favour

intense crown fires (Pausas et al., 2008) and are very vulnerable to recurrent wildfires that could even constrain their natural regeneration (Eugenio and Lloret, 2004; Espelta et al., 2008).

In the perspective of more extreme fire weather conditions projected for the MR, there is an urgent need for setting ecologically sound forest management strategies aiming to (i) minimize fire risk (reducing ecosystems' fire-proneness, in particular), and (ii) enhance the capacity of forests to cope with new fire regimes increasing their resistance and resilience to fire (Duguy et al., 2013). Such strategies will have to integrate a wide array of stand structure adaptation and fuel control techniques.

In this context, our study intends to gain further insights into short-term effects on the understory vegetation of a spring prescribed burning conducted under a *P. halepensis* canopy. The goal is to contribute to a more comprehensive assessment of this technique's suitability in relation to the promotion of more sustainable and adaptive management practices for Aleppo pine forests in Eastern Spain.

2. Materials and methods

2.1. Study area

The study was conducted in a *Pinus halepensis* forest planted in 1970 over abandoned crops (Vega-García et al., 2014) in the Colladetes area (UTM Zone 31N: 304762, 4530927), which is located in the municipality of El Perelló (Southern Catalonia, Northeastern Spain) (Fig. 1). The altitude range is 238–250 m·a.s.l. The climate is Mediterranean (Sánchez de Dios et al., 2009; Casals et al., 2016), with a mean annual temperature of 16.5 °C and a mean annual precipitation of 504 mm, after data registered by the nearest weather station (El Perelló) for the (1973–2013) period (http://www.aemet.es/). The annual water deficit is 300–400 mm, which is aggravated by frequent dry NW winds reaching a mean annual speed of 9.5 m·s^{-1} and maximum speeds sometimes overpassing 30 m·s^{-1} (POUM El Perelló, 2010). These are some major factors contributing to the high fire-proneness that characterizes the studied forest most part of the year.

The dominant soils, generally shallow (<50 cm), are *Lithic xerorthents* and *Lithic haploxerepts* (Soil Survey Staff, 2010), developed over limestones and dolomites (Duguy et al., 2015).The current landscape mosaic, resulting from centuries of human activity, is dominated by rainfed crops (olive trees, cereals), shrublands (mostly dominated by *Quercus coccifera* L., *Pistacia lentiscus* L. and *Rosmarinus officinalis* L.) and *Pinus halepensis* forests. The latter are generally occupying former agricultural lands that were abandoned throughout the XXth century (Vega-García et al., 2014). The pine forests' understory is composed by *Querco-Lentiscetum* Br.-Bl. et al., 1935 *em.* A. *et* O. Bolòs 1950 macchia, dominated by *P. lentiscus* and *Q. coccifera*, and *Rosmarino-Ericion* Br.-Bl. 1931 shrublands, dominated by *R. officinalis* and *Erica multiflora* L., with the presence of *Ulex parviflorus* Pourr. (Duguy et al., 2015). The herbaceous layer is dominated by *Brachypodium retusum* (Pers.) P. Beauv.

Throughout the second half of the XXth century, land abandonment led to an increase in fuel amount and continuity in this landscape, promoting its fire-proneness. Although in the last decade in the Baix Ebre subregion, in which El Perelló is located, there was only one fire larger than 500 ha (i.e. the Rasquera fire that reached 2800 ha in May 2012; https://www.idescat.cat/), nine of its fourteen municipalities (El Perelló, in particular) are qualified as high fire risk municipalities by the fire prevention administration (http://agricultura.gencat.cat/ca/ambits/medi-natural/). This assessment is based on field-collected fuel moisture measures, meteorological forest fire risk indices, historical fire occurrence, fuel model maps and vegetation flammability maps.

2.2. Vegetation sampling and characterization

Three 10 × 10 m permanent plots were randomly located in a flat pine stand where the Forest Actions Support Group (GRAF) of the Autonomous Catalan Government (Casals et al., 2016) had planned to
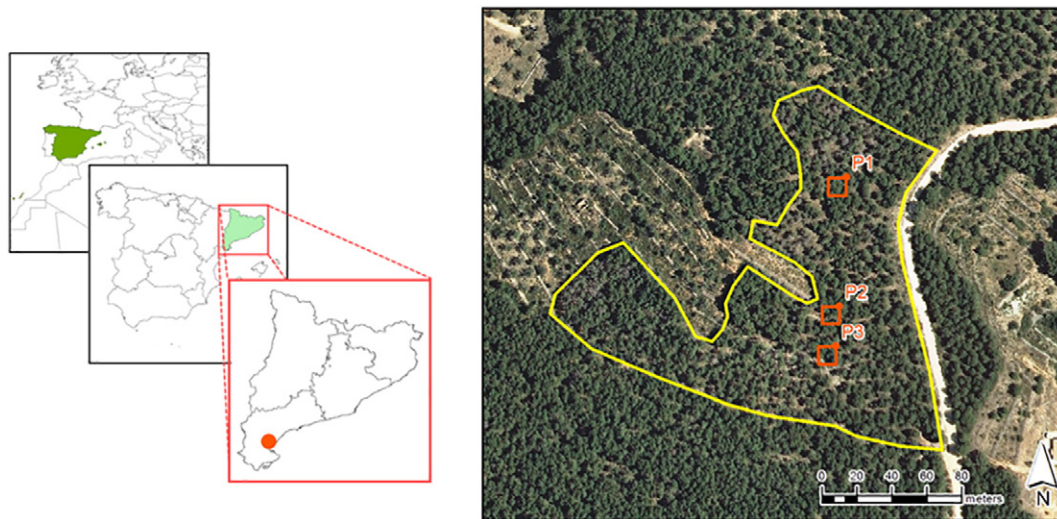
Fig. 1. Location of El Perelló municipality (red dot) and sampling plots (red squares) within the perimeter of the prescribed burning (yellow line) conducted in May 2013.

conduct a spring understory prescribed burning, which was finally conducted in May 2013. Each plot was divided in a regular matrix of one hundred 1 m² quadrats. The understory vegetation sampling was carried out in February 2013 (Control) and repeated in March 2014 (Burnt); i.e. before and 10 months after the burning, respectively.

In each quadrat, we recorded the species composition (list of present plant species), estimated the herbaceous and shrub percentage covers and measured several variables for each shrub: maximum height, crown base height and maximum and minimum crown diameters; recording the vitality (living/dead) of each measured individual. After these field-collected variables, we established for each plot the species richness (total and by functional groups) and computed both the Shannon-Wiener's diversity (Krebs, 1989) and the Sørensen's floristic similarity (Brower et al., 1997) indices. In relation to species richness, three functional groups were considered: herbaceous/woody, the post-fire regeneration strategy (resprouter/seeder; according to Duguy and Vallejo, 2008; Paula and Pausas, 2013), and the Raunkiær life form (after Bolòs et al., 2005).

The Shannon-Wiener's diversity index was calculated as follows: $H' = - \sum_{i=1}^{S} p_i \log_2 p_i$, where S is the total number of species and p_i is the relative abundance of species i in the plot (measured as the frequency of that species in the plot divided by the summation of all the species' frequencies in that plot).

The Sørensen's floristic similarity index, calculated as $IS = \frac{2C}{A+B} * 100$, compares two communities in relation to the presence-absence of species considering the number of species in each community (A and B) and the number of species present in both (C). As for the structural variables, we computed for each plot the mean values of herbaceous and shrub percentage covers as the mean of all the corresponding quadrat cover values. We estimated for each quadrat and plot the mean shrub height (H), i.e. mean height of the shrub layer, and the maximum height (Hmax) for each present dominant shrub species (*E. multiflora*, *P. lentiscus*, *Q. coccifera*, *R. officinalis* and *U. parviflorus*). Only living individuals were considered and quadrats without shrubs (or without the species) were discarded.

Besides, the frequency of each species was estimated for each plot according to the following expression:

$$\%Freq_i = \frac{\text{number of quadrats with species } i}{100 \text{ quadrats}} * 100$$

Apparent total and apparent crown volumes (ATV and ACV, respectively) were estimated for all measured shrubs after the field-collected

dimensional variables and using the ellipsoidal cylinder geometric shape. This shape proved to be suitable for estimating the volumes of the shrub species dominating in our site since it generally led to well-fitting regression equations between the apparent volume and any aboveground phytomass fraction (Godoy, 2014; Duguy et al., 2015). In each plot, the apparent volumes of all living individuals were added to obtain the total living ATV and ACV.

As for the dead standing shrub volume, we considered both dead standing shrub individuals and dead twigs in living individuals. The apparent volumes of the former were estimated in the same way as for the living shrubs, whereas the volume of each dead twig was computed as a cylinder using its longitude and a mean diameter of 1 cm that was considered as representative of dead twigs present in Burnt plots after measuring the diameter of 100 dead twigs (randomly selected among individuals of all dominant shrub species).

The aboveground living phytomasses-total, fine (ø < 0.6 cm) and coarse (ø > 0.6 cm) fractions were estimated for each measured shrub applying the corresponding apparent volume-aerial phytomass specific allometric equation previously established in this plant community both with ATV and ACV (Godoy, 2014; Duguy et al., 2015). The obtained phytomasses were always larger when applying the allometry with ACV. We decided, thus, to work with the crown volumes in order to counterbalance (presumably to a large extent) the underestimation of total aerial shrub phytomass deriving from the fact that only the five dominant shrub species in the shrub layer were considered through the established allometries. Furthermore, in the perspective of a future use of these aerial phytomass data for characterizing the associated fire behavior fuel models and, thus, modeling fire, it seemed preferable to work with the largest phytomass estimations (i.e. the worst scenarios in terms of fuel load and therefore potential fire intensity).

In the case of *E. multiflora* allometric equations, the regression coefficient was good ($r^2 = 0.77$) for total phytomass but low ($r^2 < 0.5$) for both fine and coarse fractions. For estimating these two latter fractions, we therefore used the percentage distribution of fuel load by diameter fraction applied by Fernandes and Pereira (1993) for *Erica arborea*, assuming that the proportions of the two fractions in relation to the total aboveground phytomass are similar in both species.

Considering all adult individuals of the 5 dominant shrub species in each plot, we finally obtained an estimation of the aboveground living shrub phytomasses per plot (total and sorted into fine and coarse fractions). In Burnt plots, the phytomasses of *P. lentiscus* resprouts and *R. officinalis* seedlings were also considered and estimated using the corresponding allometric specific equations. *Q. coccifera* resprouts were short

(generally <10 cm), which made it difficult to apply these equations. Their phytomass was estimated with the equation proposed by Montès et al. (2004) that relates the resprouts' cover with their aerial phytomass in 3 years old *Q. coccifera* shrublands. The *Q. coccifera* resprouts cover per quadrat was always around 40% (when they were present) and we reduced by half the phytomass obtained with the formula, as the resprouts in our Burnt plots were only 1 year old.

As for dead standing shrub phytomasses (total and sorted into fine and coarse categories), they were estimated applying the already mentioned allometric equations to the corresponding aerial dead standing volumes.

The obtained total, fine and coarse aboveground phytomass values (TAP, FAP and CAP, respectively) had a little built-in bias depending on the r^2 coefficient of each allometric equation. FAP and CAP needed, thus, to be corrected in order to meet the equality TAP = FAP′ + CAP′. Following the approach proposed by Montero et al. (2005) for tree's phytomass, FAP′ and CAP′ were obtained as follows: FAP′ = $\frac{FAP}{(FAP+CAP)}$*TAP and CAP′ = $\frac{CAP}{(FAP+CAP)}$*TAP.

2.3. Data analysis

In the case of variables for which we only estimated one value per plot (i.e. species richness, Shannon-Wiener's diversity index, volume and phytomass fractions), the Treatment factor (2 levels, Burnt (B) and Control (C)) was the only considered. A Student's *t*-test for paired samples was used to check for significant differences due to burning (significance when p < 0.05), except in the case of species frequencies for which we carried out a Chi-square test for comparing each plot's situation before and after burning.

Moreover, a non-metric multidimensional scaling (NMDS) ordination analysis (Kruskal, 1964) using Bray-Curtis distance (Bray and Curtis, 1957) was conducted with species' frequencies for all plots and the two levels of the Treatment factor. The goal here was to visualize the dissimilarities in species' frequencies among plots and treatments in order to understand in which way PB affected such dissimilarities, enhancing or not the heterogeneity in relation to species' frequencies.

For cover- and height-related variables, we estimated one value for each of the 100 quadrats inside the plot. In the case of herbaceous and shrub percentage covers, a zero-inflated Poisson (ZIP) (Lambert, 1992) generalized linear model was fit for studying the differences between Control and Burnt plots. This model has been successfully applied for modeling ecological count data with excess zero values (Welsh et al., 1996; Cunningham and Lindenmayer, 2005). It is based upon a two-component model that combines a binomial probability of observing zero values, and a Poisson distribution-based generalized linear model (GLM) for data larger than 0. The factors Treatment (2 levels) and Plot (3 levels), as well as their interaction, were considered in the analysis. Both parts of the model (binomial and Poisson) used the two factors and their interaction. The final score of the ZIP model is reached by multiplying the Poisson GLM score by the probability of observing zero values given by the binomial component.

As for shrub height, we modeled the differences between Control and Burnt plots for both mean height (H) and maximum height (Hmax) variables using a GLM with a Poisson error distribution (GLM-P). In this case, we did not want to study changes in the horizontal occupation of the vegetation but explore if the burning caused strong alterations in the shrub layer height that would affect, in turn, both shrub aboveground phytomass and its vertical distribution. The continuity between shrub layer fuels and tree canopy is a particularly crucial structural property in relation to fire behavior. We therefore only took into account quadrats in which shrubs were present (i.e. zero values were not considered in these analyses). We applied a two factor GLM-P, with Treatment (2 levels) and Plot (3 levels) being the factors, and the quadrats where a shrub layer was present being considered as observations.

For each dependent variable, the Akaike Information Criterion corrected for small sample size, or AICc (Burnham and Anderson, 2002), was used for selecting the most informative model (or best model) among all candidate models, including the null model. Based on Paredes et al. (2015), we considered that differences larger than 2 in the AICc value between two models implied that the model with the largest value was less informative and could be omitted. In this study, for a given response variable, we only report the estimates and standard errors of the model with lowest AICc. For each selected model, we visually checked both its general performance (plotting the quantile-quantile plot) and its errors distribution related to observations in order to avoid heteroscedasticity. If any trend was observed for the model errors, either we changed the link function, or transformed the response variable, or did both things in order to make the model errors homogeneous through observations.

Deviance measures the discrepancy between modeled and observed data. We computed the decrease in deviance (DI) obtained using the best model (Dm) compared to the Null model (Dn) following the eq. DI = (Dn − Dm) / Dn * 100. It ranges between 0 and 100, where 0 corresponds to a model that is not more informative than the null model, and 100 corresponds to a model that explains all the information contained in the data.

We used PRIMER 6 software (version 6.1.11; Primer-E Ltd., Plymouth, UK) for performing the NMDS. The rest of analyses were conducted in the R environment (R Development Core Team, 2016, version 3.3.2). ZIP analyses were performed with the "zeroinfl" function within the "pscl" package (Jackman, 2015). GLM-P analyses were run with the "glm" function (Dobson and Barnett, 2008).

3. Results

3.1. Species richness, diversity and floristic composition

In Control (C) and Burnt (B) plots, we found 34 and 25 species, respectively (Table 1). Globally, 36 species were identified: 15 herbaceous and 21 woody species. Mean total species richness was smaller one year after the prescribed burning (26.3 ± 4.9 in C and 18 ± 1.7 in B), but not significantly (*t* = 2.3623, p = 0.142) (Table 2). Both mean herbaceous richness (11 ± 3 in C and 6.7 ± 1.5 in B; *t* = 1.8028, p = 0.2132) and mean woody species richness (15.3 ± 2.5 in C and 11.3 ± 2.1 in B; *t* = 3.4641, p = 0.0742) decreased. We also observed non-significant decreases in richness when grouping species by post-fire regeneration strategy (Table 2). Mean seeders richness decreased from 8.7 ± 3.8 in C to 2.7 ± 2.1 in B plots (*t* = 2.6458, p = 0.1181), and mean resprouters richness from 17.7 ± 1.2 in C to 15.3 ± 0.6 in B plots (*t* = 2.0785, p = 0.1732). Globally, the total number of seeders among all plots strongly decreased with the treatment (from 14 to 5 species), whereas the number of resprouters (19 species) did not change.

As for the Raunkiaer life forms, the mean richness always decreased (Table 2); the effect being significant only for the Nanophanerophytes (8.7 ± 0.6 in C and 6.3 ± 0.6 in B; *t* = 7, p = 0.0198). Considering the total number of species among all plots, the strongest reductions in richness corresponded to the Hemicriptophytes and Geophytes (47% and 50%, respectively). The biological spectrum of the community (i.e. distribution of the number of species per life form) was almost not altered by the treatment. Globally, the Chamaephytes remained the most abundant life form, followed by the Nanophanerophytes and Hemicriptophytes, whereas the Therophytes were always the least abundant form (no Therophyte was observed among Burnt plots). Hemicriptophytes and Chamaephytes were the most represented forms among herbaceous, and Chamaephytes followed by Nanophanerophytes the most represented among woody species. These distributions were not altered by the treatment.

The PB caused a decrease of the Shannon-Wiener diversity index (3.7 ± 0.3 in C and 2.7 ± 0.2 in B; *t* = 4.0948, p = 0.0547). The strong decrease of seeders undoubtedly contributed to that effect. No seeder

Table 1
List of species identified in Control (C) and Burnt (B) plots with corresponding Raunkiaer life form, main post-fire regenerative strategy, specific frequency and occurrence. Ch: Chamae-phyte, G: Geophyte, H: Hemicriptophyte, MP: Macrophanerophyte, NP: Nanophanerophyte, Th: Therophyte. R: resprouter; S: seeder. SD: standard deviation.

Taxon	Structure	Raunkiaer life form	Post-fire strategy	Species frequency (%)				N° plots	
				C	SD	B	SD	C	B
Aphyllantes monspeliensis	Herbaceous	H	R	15,7	21,2	44,7	41,5	3	2
Asparagus acutifolius	Herbaceous	Ch	R	6,3	4,9	7	5,3	3	3
Brachypodium retusum	Herbaceous	Ch	R	88	7,2	70	21,7	3	3
Bupleurum fruticescens	Woody	Ch	S	9,7	7	0,3	0,6	3	1
Carex sp.	Herbaceous	H	R	37	1	55,7	13,3	3	3
Carlina sp.	Herbaceous	H	S	1	1	0	0	2	0
Chamaerops humilis	Woody	NP	R	2,7	2,1	2	2,6	3	2
Cirsium sp.	Herbaceous	H	S	0,7	1,2	0	0	1	0
Dactylis glomerata	Herbaceous	H	S	3,7	4,7	0	0	2	0
Dorycnium hirsutum	Woody	Ch	S	0	0	9	9,5	0	2
Erica multiflora	Woody	NP	R	30	13,5	19	9,8	3	3
Euphorbia sp.	Herbaceous	NP	S	0,3	0,6	0	0	1	0
Fumana ericoides	Woody	Ch	S	0,7	0,6	0,3	0,6	2	1
Genista scorpius	Woody	NP	S	0,3	0,6	0	0	1	0
Helianthemum sp.	Woody	Ch	S	1	1	0	0	2	0
Lathyrus sp.	Herbaceous	Th	S	0,3	0,6	0	0	1	0
Leuzea conifera	Herbaceous	H	R	9,3	4,5	4,3	4,5	3	2
Narcissus assoanus	Herbaceous	G	R	11,3	7,4	3	3	3	2
Olea europaea	Woody	MP	R	8,7	4	5	3,5	3	3
Ononis minutissima	Woody	Ch	S	0,7	0,6	2	3,5	2	1
Oprhys fusca	Herbaceous	G	R	1	1,7	0	0	1	0
Phlomis lychnitis	Woody	Ch	R	3,7	4	2,7	3,8	2	2
Pistacia lentiscus	Woody	NP	R	59,7	5,5	54,3	4	3	3
Polygala rupestris	Woody	Ch	S	1,7	2,9	0	0	1	0
Quercus coccifera	Woody	NP	R	59,0	27,2	55	28,8	3	3
Rhamnus alaternus	Woody	Ch	R	27,7	12,4	25	6,6	3	3
Rhamnus lycioides	Woody	NP	R	1,7	0,6	1,3	1,5	3	2
Rosmarinus officinalis	Woody	NP	S	42,7	9,3	7	7,5	3	2
Rubia peregrina	Herbaceous	NP	R	12,7	9,9	14	12,1	3	3
Santolina chamaecyparissus	Woody	Ch	S	1	1,7	0	0	1	0
Sonchus tenerrimus	Herbaceous	Ch	S	1,7	2,9	0	0	1	0
Stipa offneri	Herbaceous	H	R	59,3	34,3	7	6,1	3	2
Teucrium chamaedrys	Woody	Ch	R	2	2	3,7	4,7	2	2
Thymus piperella	Woody	Ch	R	0	0	1	1,7	0	1
Thymus vulgaris	Woody	Ch	R	16,7	12,1	0,7	0,6	3	2
Ulex parviflorus	Woody	NP	S	19,0	16,5	1	1,7	3	1

herbaceous species was observed after the treatment and seeder woody species decreased (33.3%). Among the 4 woody species apparently disappearing after the PB, all were seeders (Table 1): 3 Chamaephytes (*Helianthemum* sp., *Polygala rupestris*, *Santolina chamaecyparissus*) and 1 Nanophanerophyte (*Genista scorpius*).

Considering all species, the ratio number of seeders/number of resprouters clearly decreased wih the burning (from 0.8 to 0.3). Grouping species by life forms, that same ratio decreased around 50% for both Chamaephytes and Nanophanerophytes. Seeder Hemicriptophytes disappeared (i.e. *Carlina* sp., *Cirsium* sp. and *Dactylis glomerata*).

Table 2
Total species richness in the sampled plots (P1, P2, P3) and species richness grouped by herbaceous and woody species, by main post-fire regenerative strategy (R: resprouter: S: seeder) and by Raunkiaer life form. Ch: Chamaephyte, G: Geophyte, H: Hemicriptophyte, MP: Macrophanerophyte, NP: Nanophanerophyte, Th: Therophyte. SD: standard deviation.

	Total	Herbaceous	Woody	R	S	Ch	G	H	MP	NP	Th
				Control							
P1	24	11	13	17	7	7	1	6	1	9	0
P2	32	14	18	19	13	12	2	7	1	9	1
P3	23	8	15	17	6	9	1	4	1	8	0
Mean	*26,3*	*11*	*15,3*	*17,7*	*8,7*	*9,3*	*1,3*	*5,7*	*1*	*8,7*	*0,3*
SD	*4,9*	*3,0*	*2,5*	*1,2*	*3,8*	*2,5*	*0,6*	*1,5*	*0*	*0,6*	*0,6*
				Burnt							
P1	17	8	9	16	1	5	1	4	1	6	0
P2	17	5	12	15	2	7	0	2	1	7	0
P3	20	7	13	15	5	9	1	3	1	6	0
Mean	*18*	*6,7*	*11,3*	*15,3*	*2,7*	*7*	*0,7*	*3*	*1*	*6,3*	*0*
SD	*1,7*	*1,5*	*2,1*	*0,6*	*2,1*	*2*	*0,6*	*1*	*0*	*0,6*	*0*

The Shannon-Wiener's diversity of a community accounts for both abundance and evenness of the present species. In that sense, it was also influenced by the strong changes in species frequencies that took place in our plots and were shown by both the chi-square test and the NMDS analysis (Fig. 2). The latter led to a clear separation of plots, characterized by their specific frequencies, according to the level of Treatment (Control or Burnt). Control plots are characterized by large frequencies of several species whose presence appears to be strongly reduced by burning (*R. officinalis* and *Stipa offneri*) (Table 1). Burnt plots are characterized by large frequencies (in relation to Control) of several other species, mostly Hemicriptophytes (*Aphyllantes monspeliensis* and *Carex* sp.). In the case of the 2 dominant seeder shrubs in Control plots (i.e. *R. officinalis* and *U. parviflorus*), frequencies strongly decreased (83.6 and 94.7%, respectively). In contrast, decreases in frequency were small for the 2 dominant resprouter shrubs (*P. lentiscus* and *Q. coccifera*; 9 and 6.8%, respectively) (Table 1). As for the herbaceous layer, the largest frequency increases caused by burning were observed for 3 resprouters; *A. monspeliensis*, *Teucrium chamaedrys* and *Carex* sp. (185, 83.5 and 50.5%, respectively).

The Sørensen index reached 78%, reflecting a high similarity between the two communities in relation to floristic composition. Indeed, 64% of the 36 identified species (i.e. 23 species) were present both before and after the PB.

Only 2 species were found exclusively in Burnt plots (*Dorycnium hirsutum* and *Thymus piperella*), whereas 11 species apparently disappeared with the treatment (Table 1). Among the latter, we found 7 herbaceous taxa (*Carlina* sp., *Cirsium* sp., *Dactylis glomerata*, *Euphorbia* sp., *Lathyrus* sp., *Ophrys fusca* and *Sonchus tenerrimus*) and 4 woody species, as already commented (Table 1). These 11 species were never abundant
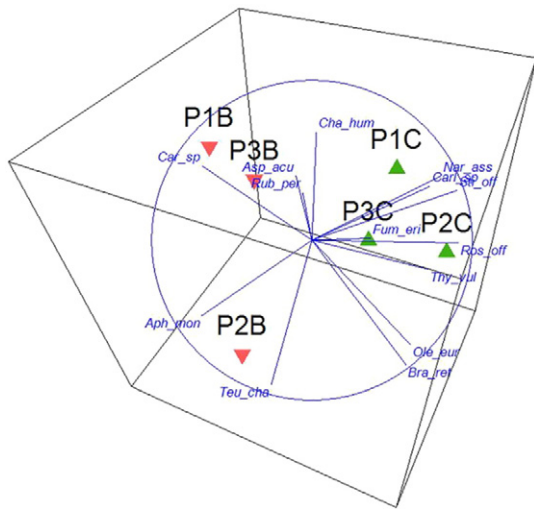
Fig. 2. 3D representation of NMDS analysis results for species' frequencies for all plots and the two levels of the Treatment factor (Control/Burnt, green/red triangles, respectively). Species with a Pearson correlation with the axes > 0.9 are represented in blue. *Aphyllanthes monspeliensis* (Aph_mon), *Asparagus acutifolius* (Asp_acu), *Brachypodium retusum* (Bra_ret), *Carex* sp. (Car_sp), *Carlina* sp. (Carl_sp), *Chamaerops humilis* (Cha_hum), *Fumana ericoides* (Fum_eri), *Narcissus assoanus* (Nar_ass), *Olea europaea* (Ole_eur), *Rosmarinus officinalis* (Ros_off), *Rubia peregrina* (Rub_per), *Stipa offneri* (Sti_off), *Teucrium chamaedrys* (Teu_cha), *Thymus vulgaris* (Thy_vul).

in Control plots though (reaching a maximum mean cover of 3.7%), and were generally only present in one of the three (C) plots.

It is noteworthy that 56% of the species found among the Control plots were in the 3 (C) plots, while only 36% of the species found among the Burnt plots were present in the 3 (B) plots.

3.2. Vegetation structural variables

Total shrub volume was significantly smaller after the burning (1454 $\pm$ 377 m^3/ha in C and 797.8 $\pm$ 171 m^3/ha in B; $t = 5.3086$, p = 0.0318) (Table 3). Living shrub volume significantly decreased too (1429.6 $\pm$ 355.5 m^3/ha in C and 605.5 $\pm$ 155.6 m^3/ha in B; $t = 6.7497$, p = 0.02125), whereas dead standing shrub volume (i.e. dead shrub individuals and dead standing twigs) became near to 8 times larger (24.4 $\pm$ 22.9 m^3/ha in C and 192.3 $\pm$ 31.1 m^3/ha in B; $t = -9.2969$, p = 0.01137) (Table 3).

Resulting from the reduction of the living shrub volume, both total shrub phytomass and living shrub phytomass decreased significantly.

The former was reduced by 49% (7.26 $\pm$ 1.76 Mg/ha in C and 3.67 $\pm$ 0.5 Mg/ha in B; $t = 4.3515$, p = 0.0489) and the latter by 61% (7.2 $\pm$ 1.7 Mg/ha in C and 2.81 $\pm$ 0.68 Mg/ha in B; $t = 4.8071$, p = 0.0407) (Table 4).

Fine living shrub phytomass was reduced by 60% (4.57 $\pm$ 1.42 Mg/ha in C and 1.82 $\pm$ 0.48 Mg/ha in B) and coarse living shrub phytomass by 62% (2.63 $\pm$ 0.3 Mg/ha in C and 0.99 $\pm$ 0.24 Mg/ha in B); the latter decrease being significant ($t = 10.2911$, p = 0.0093). The fine/coarse living shrub phytomass ratio was maintained after the burning; 1.7 $\pm$ 0.4 and 1.8 $\pm$ 0.3 in Control and Burnt plots, respectively. We observed a reduction in living phytomass for all shrub dominant species, being *U. parviflorus* (which lost practically all its living phytomass), *E. multiflora* (reduction of 96.7%), *R. officinalis* (95.6%) and *Q. coccifera* (89.3%) the most affected species. *P. lentiscus* only lost 25.6% of its living phytomass and clearly increased its dominance in relation to total living phytomass. It accounted for 48.6% of the total living shrub phytomass among (C) plots and 92.5% among (B) plots. The *t*-tests only detected a significant change in living phytomass for *E. multiflora*, though (1.4 $\pm$ 0.8 Mg/ha in C and 0.04 $\pm$ 0.004 Mg/ha in B; $t = 9.55$, p = 0.0108).

Contrarily, dead standing shrub phytomass significantly increased in the short term (0.06 $\pm$ 0.07 Mg/ha in C and 0.85 $\pm$ 0.27 Mg/ha in B; $t = -4.9394$, p = 0.0386), being > 10 times larger in Burnt plots (Table 4). It was quite variable, though, especially among Control plots, and also depending on the species. It increased both for fine (0.04 $\pm$ 0.04 Mg/ha in C and 0.54 $\pm$ 0.27 Mg/ha in B) and coarse (0.02 $\pm$ 0.03 Mg/ha in C and 0.31 $\pm$ 0.11 Mg/ha in B) fractions, resulting in a non-significant decrease of the fine/coarse dead standing shrub phytomass ratio; 4.6 $\pm$ 6 and 2 $\pm$ 1.6, before and after the burning, respectively ($t = 0.6236$, p = 0.5966). It is remarkable that *U. parviflorus* dead standing biomass was inexistent one year after the burning, while it reached 0.008 $\pm$ 0.015 Mg/ha in Control plots.

As for Mean shrub height (H) and Maximum shrub height (Hmax) variables, which were estimated at the quadrat level, the most parsimonious corresponding models included both factors (Treatment, Plot) and their interaction (Table 5). Globally, H clearly decreased (51%) and the strongest decrease was observed in P2 (56%). Both before and after the burning, P2 and P3 exhibited the smallest and largest H values, respectively (Table 3).

Similar effects were observed for the maximum height of *P. lentiscus*, which was reduced by the burning (17%), with P2 and P3 being also characterized by the smallest and largest values, respectively, both before and after the burning. Quite strong decreases were observed for P2 and P3 (25.6% and 23.6%, respectively), whereas the variable remained stable in P1. This species reached the largest Hmax value among all dominant shrubs, both before and after the burning (0.65 $\pm$ 0.29 m and 0.54 $\pm$ 0.34 m, respectively).

Table 3

Mean shrub height and Maximum shrub height (in metres), mean shrub phytovolumes (total, living and dead standing fractions) in m^3/ha, and mean shrub and herbaceous percentage covers (in %) in the sampled plots (P1, P2, P3). SD: standard deviation.

	Shrub height (H)		Maximum shrub height (Hmax)		Shrub phytovolume			Shrub cover		Herbaceous cover	
	Mean	SD	Mean	SD	Total	Living	Dead	Mean	SD	Mean	SD
					Control						
P1	0,47	0,22	0,61	0,27	1887,5	1839,2	48,4	57,9	28,2	49,2	30,7
P2	0,37	0,18	0,51	0,26	1202,9	1200	2,9	35,8	23,6	55,9	29,2
P3	0,63	0,31	0,66	0,33	1271,7	1249,7	22	34,5	25,5	49,5	27,2
Mean	*0,49*		*0,6*		*1454*	*1429,6*	*24,4*	*42,7*		*51,5*	
SD		*0,27*		*0,29*	*377*	*355,5*	*22,9*		*27,9*		*29,2*
					Burnt						
P1	0,26	0,29	0,29	0,32	991,4	773,4	218	23,1	25,6	8,9	10,3
P2	0,16	0,24	0,17	0,26	667,2	466	201,2	11,4	17,8	9	6,6
P3	0,30	0,34	0,33	0,38	734,8	577	157,8	17,6	22,9	16,5	13,4
Mean	*0,24*		*0,27*		*797,8*	*605,5*	*192,3*	*17,4*		*11,5*	
SD		0,30		0,33	171	155,6	31,1		22,7		11

Table 4

Total, fine (ø < 0.6 cm) and coarse fractions of mean shrub phytomass, mean living shrub phytomass and mean standing dead shrub phytomass (in Mg/ha). SD: standard deviation.

	Aboveground shrub phytomass			Living shrub phytomass			Dead standing shrub phytomass		
	Total	Fine	Coarse	Total	Fine	Coarse	Total	Fine	Coarse
					Control				
P1	9,24	6,27	2,97	9,10	6,19	2,91	0,14	0,08	0,06
P2	6,67	4,02	2,65	6,66	4,01	2,65	0,01	0	0
P3	5,88	3,55	2,33	5,84	3,51	2,32	0,04	0,03	0
Mean	*7,26*	*4,61*	*2,65*	*7,20*	*4,57*	*2,63*	*0,06*	*0,04*	*0,02*
SD	*1,76*	*1,45*	*0,32*	*1,70*	*1,42*	*0,30*	*0,07*	*0,04*	*0,03*
					Burnt				
P1	4,19	2,76	1,43	3,27	2,03	1,24	0,92	0,73	0,19
P2	3,12	1,95	1,17	2,03	1,28	0,76	1,08	0,67	0,41
P3	3,69	2,38	1,31	3,14	2,16	0,98	0,56	0,23	0,33
Mean	*3,67*	*2,36*	*1,30*	*2,81*	*1,82*	*0,99*	*0,85*	*0,54*	*0,31*
SD	*0,50*	*0,41*	*0,13*	*0,68*	*0,48*	*0,24*	*0,27*	*0,27*	*0,11*

Cover-related variables were also affected by Treatment and Plot factors and their interaction (Table 6). The mean shrub and herbaceous percentage covers were clearly smaller in Burnt plots (with decreases of 59.3% and 77.7%, respectively). Shrub cover reached its largest value in P1, both before (57.9 ± 28.2%) and after the burning (23.1 ± 25.6%) (Table 3), although in the latter case the variable had been strongly reduced (60%). The largest decrease of shrub cover was registered in P2 (68.2%), though, as observed for height-related variables. This plot had the smallest post-treatment shrub cover (11.4 ± 17.8%).

The binomial component of the ZIP GLM model selected for estimating the shrub cover showed that the probability of observing zero values among the quadrats (i.e. quadrats with no shrub cover) strongly increased after burning (230%) and in all plots.

In the case of the herbaceous cover, the decreases caused by the burning were even larger; 81.9%, 83.9% and 66.7% in P1, P2 and P3, respectively. P2 was characterized by the largest pre-burning and the second smallest post-burning herbaceous cover; 55.9 ± 29.2% and 9 ± 6.6%, respectively (Table 3). The binomial component of the ZIP GLM model showed, however, that the probability of observing zero values among the quadrats only increased in one plot (P1), but very strongly (197%). It decreased, on the contrary, in P2 and P3 (79% and 87%, respectively).

Table 5

Mean and standard error (SE) for the coefficients of GLM-P analysis upon Mean shrub height (H) and Maximum shrub height (Hmax). DI: decrease in deviance obtained using the best model compared to the Null model. C: Control; B: Burnt. P1, P2 and P3 are the plots. Coefficients' nomenclature is based on R software output in order to facilitate their interpretation.

Coefficient	Mean	SE	n	DI (%)
		H		
P1-B	3.781	0.02		
C	0.032	0.03		
P2	−0.376	0.04		
P3	0.177	0.03		
P2-C	0.282	0.05		
P3-C	0.226	0.04	252	17
		Hmax		
P1-B	3.86	0.02		
C	0.195	0.03		
P2	−0.405	0.04		
P3	0.184	0.03		
P2-C	0.383	0.05		
P3-C	0.013	0.04	252	18.9

Table 6

Mean and standard error (SE) for the coefficients of ZIP-GLM analysis upon herbaceous and shrub percentage covers. Both the Poisson and Binomial sub-models coefficients are indicated. DI: decrease in deviance obtained using the best model compared to the Null model. C: Control; B: Burnt. P1, P2 and P3 are the plots. Coefficients' nomenclature is based on R software output in order to facilitate their interpretation.

Herbaceous percentage cover					Shrub percentage cover				
Poisson	Mean	SE	n	DI (%)	Poisson	Mean	SE	n	DI (%)
P1-B	2.3	0.03			P1-B	3.18	0.03		
C	1.64	0.05			C	0.89	0.03		
P2	−0.08	0.05			P2	−0.54	0.04		
P3	0.51	0.04			P3	−0.07	0.03		
P2-C	0.26	0.05			P2-C	0.14	0.04		
P3-C	−0.48	0.05			P3-C	−0.38	0.04		
Binomial	Mean	SE	n	DI (%)	Binomial	Mean	SE	n	DI (%)
P1-B	−2.09	0.31			P1-B	−3.18	0.51		
C	−1.09	0.6			C	−1.41	1.12		
P2	−1.81	0.79			P2	1.73	0.57		
P3	−2.5	1.05			P3	1.85	0.56		
P2-C	2.67	1			P2-C	0.55	1.21		
P3-C	3.1	1.24	600	50	P3-C	0.16	1.21	600	22

4. Discussion

4.1. Species richness, diversity and floristic composition

We observed short-term decreases of species richness and diversity after the burning, although not significant. These results do not seem in accordance with the increase in species richness often observed in Mediterranean-type ecosystems in the first stages (1–2 years) of post-fire secondary succession (Kazanis and Arianoutsou, 1996; Guo, 2001). After a fire new open spaces created by the perturbation allow the establishment of opportunistic species (particularly annuals or short-lived perennial species) that benefit from the larger availability of resources (light, nutrients) and the reduction of interspecific competition (Trabaud, 1994; Arianoutsou and Thanos, 1996; Clemente et al., 1996; Kazanis and Arianoutsou, 1996; Guo, 2001). These species are often Therophytes, which may even dominate the first years after a fire (Kazanis and Arianoutsou, 1996; Guo, 2001).

In our control plots, species dominating the herbaceous layer were perennial species, mostly Hemicriptophytes and Chamaephytes. Only one Therophyte was observed. This life form is apparently scarce, thus, in the sampled pine forest, which likely results from inadequate light conditions in the understory, maybe combined with effects of past management practices. The canopy cover of this stand, which is spatially variable and estimated between 50 and 80% (Valor 2014, personal communication), was not altered by the burning. Since the tree layer remained unburned, light conditions did not become favourable enough for the establishment of new species (herbaceous, in particular), in spite of the substantial decrease of shrub cover (spatially heterogeneous, though, reflecting the heterogeneity of the burning itself). Besides, many species dominating the herbaceous and shrub layers before the burning were vigorous resprouters, such as *B. retusum* or *Q. coccifera* (Papió, 1994; Pausas et al., 1999; Delitti et al., 2005), which rapidly reoccupied the spaces opened by the treatment. Moreover, several other resprouters increased their frequency with the treatment (mostly Hemicriptophytes, such as *A. monspeliensis* and *Carex* sp.).

Studies documenting strong short-term increases in species richness after a wildfire (Kazanis and Arianoutsou, 1996; Crawford et al., 2001; Keeley et al., 2005) or a burning (Carreira et al., 1992) were mostly conducted in plant communities with no tree layer, or after fires causing strong changes in the canopy cover, therefore altering understory conditions (light availability particularly). Many authors working in coniferous forest ecosystems have documented the relationship existing between canopy cover and understory richness or abundance (herbaceous cover in particular) (Pase, 1958; Laughlin and Fulé, 2008; Sabo

et al., 2009; Scudieri et al., 2010), observing that only a strong canopy opening may allow significant changes in the understory vegetation (Sabo et al., 2009; Scudieri et al., 2010; Arévalo et al., 2014).

Besides, several studies that monitored short term effects of low intensity PB on understory vegetation in Mediterranean pine plantations, but also in broadleaf forests, observed, as in our case, little effects on species richness and composition (Catalanotti, 2009; Ascoli and Bovio, 2013). The low intensity of the burning, which is apparently a common feature between these studies and ours, could be another cause explaining the low presence of annual and biennial species in our Burnt plots.

Fire behavior (intensity, in particular), which was not monitored in our study, is a factor that interacts with the pre-disturbance vegetation determining the post-fire response (Moreno and Oechel, 1994; Griffis et al., 2001; Knapp et al., 2007; Duguy and Vallejo, 2008). The persistence of fire-promoted species has been positively associated, indeed, with fire intensity measures (Knapp et al., 2007). In our burnt plots, we found adult individuals that survived to burning for all dominant shrub species but for *U. parviflorus*, and with high rates of survival for the two most frequent ones (*P. lentiscus*, *Q. coccifera*). It suggests that the burning intensity was low-to-moderate, but nevertheless effective for controlling *U. parviflorus* in the short term. No seedlings of that species were found in Burnt plots.

Both *R. officinalis* and *U. parviflorus* are fire-stimulated recruitment species that generate persistent soil seed banks (Roy and Sonié, 1992). The germination of these seeds is stimulated by the heat released by fire and penetrating into the mineral soil. As soil seed banks were probably not depleted in the studied stand, in which no fires took place in recent years, it is likely that the heat pulse generated by our burning was not intense enough to break the dormancy of high proportions of stored seeds.

Besides, low intensity fires do not consume fuels over a large percentage of the forest floor, hence not exposing mineral soil and not favouring seed germination (Knapp et al., 2007; Sabo et al., 2009).

The non-consumed litter, although never reaching a large depth in our plots, also contributed, probably, to the low recruitment of seeder shrubs (of *U. parviflorus* particularly). It is known that litter layer, or any plant remain on the soil surface, interact with plant germination and/or growth (Pérez and Moreno, 1998; Knapp et al., 2007). Plant remains on the ground act as a mulch that may reduce germination through a buffering of soil surface temperature fluctuations, and limit seedling development through physical impedance and reduction of light intensity (Baeza and Roy, 2008). Experiments carried out in Eastern Spain shrublands have shown that leaving plant residues from clearing (slash) on the ground may negatively affect *U. parviflorus* reducing its germination (Baeza and Roy, 2008; Valdecantos et al., 2009). It is noteworthy that slash effect on recruitment is differential. It may favour, on the contrary, the establishment of resprouting species that have stored reserves allowing their growing through the mulch layer, as observed for *Q. coccifera* (Baeza and Roy, 2008).

Weather conditions, and precipitation levels in particular, strongly influence the post-fire vegetation response too (Pausas et al., 1999; Moreno et al., 2011). In our study area, the fall (September–November), and particularly the winter (December–March), after the burning were quite dry. The accumulated precipitation was 152 and 74 mm, respectively, smaller than the average values registered for these two periods considering the historical rainfall series (1973–2013); i.e. 177 and 147 mm, respectively. Furthermore, during the months preceding the post-fire field sampling (January–March 2014), the accumulated precipitation was only 62 mm, in contrast with the average value of 104 mm for the (1973–2013) period (http://www.aemet.es/).

Undoubtedly, the scarcity of precipitations did not facilitate the establishment of annual species after the burning. It probably also affected the recruitment of perennial seeders present in the pre-fire community. Seed germination is strongly dependent on environmental conditions, such as light availability at soil surface and soil humidity (Roy and Sonié, 1992). In that sense, the post-fire reestablishment of perennial

seeders tends to be slower than that of resprouters and much more random (Abad et al., 1997). *R. officinalis* may have its germination delayed until the second or third year after a fire (Clemente et al., 1996; Duguy and Vallejo, 2008), particularly when post-fire months are dry (Moreno et al., 2011). Pausas et al. (1999) observed that the post-fire increase in cover of *U. parviflorus* was delayed in relation to that of resprouters, happening the second spring after a 1994 summer fire, which was characterized by a dry post-fire year.

The effect of PB on resprouter shrubs was quite variable depending on the species and the plot. This result could be due to different specific resistances to the burning, but also suggests a high spatial variability of the PB intensity and, thus, severity. This heterogeneity, which was already documented for wildfires (Lloret et al., 2002; De Luis et al., 2004) and prescribed burnings (Cassagne et al., 2011), often results, among other factors, from the multi-scale heterogeneity characterizing the pre-fire vegetation itself. The latter is, in turn, partly due to spatially and temporally variable histories of land use, management practices and disturbances (e.g. fire).

Recent studies show that fine-scale fuel heterogeneities affect fire behavior and would tend to reduce its rate of spread (Cassagne et al., 2011; Pimont et al., 2011). The final fire behavior spatial pattern strongly determines, in turn, the microvariability of the post-fire community response (De Luis et al., 2004), making the latter very difficult to predict (Duguy and Vallejo, 2008).

Erica multiflora was the most affected resprouter shrub in terms of adults survival, height and frequency reductions. Very few resprouts were found. This species is not considered as a vigorous resprouter (Lloret and López-Soria, 1993; Vilà et al., 1998). Throughout the first year after fire, its resprouting is generally slow and strongly dependent on precipitation levels (Papió, 1994; Vilà et al., 1998). As commented, the fall and early spring following the studied burning were very dry, which may also explain the low short-term post-burning recruitment of this species.

Globally, the burning promoted, however, the dominance of resprouters in the community. Although in our study the cover was not sampled discriminating the 2 post-fire regeneration strategies, our results and field observations suggest, nevertheless, that the strong reduction of seeder shrubs frequencies resulted in their smaller abundance in relation to resprouters. It is known that an increase in the abundance of resprouters (in terms of cover) in relation to seeders' promotes the community's resilience to fire (Vallejo and Alloza, 1998; Duguy and Vallejo, 2008). As commented, the post-fire reestablishment of resprouters is generally faster (Abad et al., 1997), resulting in higher plant cover recovery rates and, thus, a better control of soil erosion risk (Vallejo et al., 2009). This is a very valuable result as it confirms the possibility of promoting resilience to fire (i.e. a crucial property in fire-prone ecosystems) through the use of PB under tree canopy.

A smaller abundance of highly flammable shrub species, mostly seeders (Saura-Mas et al., 2010), is a major objective of fire prevention-oriented management in Mediterranean-type ecosystems. The studied treatment appears to be effective for reaching this goal in the short term. *U. parviflorus* is a particularly concerning species since it accumulates large loads of dead standing phytomass throughout its life cycle enhancing fire-proneness of the ecosystems (Baeza and Vallejo, 2008). Seeder shrubs dynamics in our plots needs to be followed on a longer term, though, as these species' regeneration traits generally guarantee their persistence through fires (Duguy and Vallejo, 2008; Moreno et al., 2011). Their effective control is not easy and would probably require a combination of fuel reduction techniques (including controlled burning) that should be designed on a plant community-specific basis (Baeza and Vallejo, 2008) and carried out at the appropriate spatial and temporal scales (Stephens et al., 2014; Fernandes, 2015).

No relevant changes were observed in the floristic composition, as shown by the high value of the Sørensen's Index. This is in accordance with other studies documenting that the post-fire succession model in Mediterranean forest understories is mostly determined by the pre-

fire plant community composition (Rego et al., 1991; Trabaud, 1994; Kazanis and Arianoutsou, 1996). In our case, all the species dominating the understory before the burning have co-evolved with fires developing either a high post-fire resprouting ability, or a fire-stimulated germination (Papió, 1994; Keeley et al., 2006), which generally guarantees their successful recruitment after a fire.

It is noteworthy that PB apparently promoted the spatial heterogeneity of the community in relation to species composition. This effect may be a consequence of complex interactions between the pre-treatment vegetation spatial heterogeneity and burning behavior spatial patterns. These interactions explain that, in reality, PB effects may be very variable within a single plot (Robichaud and Miller, 1999) and that a given combination of burning treatments in several plots of the same plant community may lead to different fuel reduction rates (Fernandes et al., 2000). This apparent effect of the studied burning on the species composition should be, however, further explored on a longer term and considering not only the patch scale of perception, but more scales of inquiry (Chaneton and Facelli, 1991). Besides, vegetation type and distribution determine the post-fire ash layer characteristics, influencing therefore soil hydrological responses as well (Keesstra et al., 2016). Changes in species composition caused by the PB could, thus, have further impacts after new burnings or wildfire events on the structure and function of the whole ecosystem.

4.2. Vegetation structure

For height- and cover-related variables, that were all sampled at a finer scale of observation (i.e. the quadrat), the most informative models include the interaction between Treatment and Plot factors, indicating that the characteristics of the pre-treatment vegetation, and thus all the different factors influencing its heterogeneity at various scales (e.g. past management practices), determined the effects of the burning in each plot.

The scale of observation appears to be, therefore, very relevant when analysing the effects of this type of treatments. In the case of the herbaceous cover, for instance, we observed a differential effect of PB among the plots, being P1 the only plot in which the probability of observing zero values among the quadrats increased with the burning. In that plot, the strong decrease of the two dominant herbaceous species' frequencies (i.e. *B. retusum* and *S. offneri*) was not compensated by the expansion of other species in the herbaceous layer. Contrarily, it happened in P2 and P3, as shown by our species frequencies data (Table 1) and confirmed by the NMDS analysis (Fig. 2): *Aphyllantes monspeliensis* and *Teucrium chamaedrys* frequencies strongly increased in P2 (1267% and 125%, respectively), and *Ononis minutissima* and *Carex* sp. frequencies increased in P3 (500% and 59.5%, respectively). Besides, in P3, *Dorycnium hirsutum*, which was absent before the burning, reached a post-burning frequency of 19%. Considering all plots, *Carex* sp. and *A. monspeliensis* were the third and fourth most frequent herbaceous species before the treatment (with frequencies reaching 37 and 15.7%, respectively), but far behind *B. retusum* and *S. offneri* (88 and 59.3%, respectively) (Table 1). They became the second and third most frequent herbaceous species after the burning (55.7 and 44.7%, respectively), with *B. retusum* remaining the most frequent one (70%).

In the case of shrub cover, our results clearly suggested that the burning caused a fragmentation of the shrub layer, and therefore a decrease of fuel horizontal continuity in the studied Aleppo pine stand.

Besides, it appears that for a given plot the effect of the burning may be quite different depending on the structural variable considered. In the case of P1, for instance, the treatment reducing effect was weak on mean shrub height, whereas it was strong on shrub cover and living shrub phytomass, and very strong on herbaceous cover. These results highlight the fact that an accurate characterization of the pre-burning vegetation structure conducted at the proper scale of observation may be indispensable for correctly anticipating and understanding the effects of a burning.

In general, the reductions observed in both height- and cover-related variables (much stronger in the latter case), resulted in a disruption of vertical and horizontal fuel continuities (particularly the latter) in the understory. Shrub volume and phytomass (of fine living fuels, in particular) consequently decreased too. Working in both *P. pinaster* and *P. halepensis* plantations one year after low intensity burnings, Catalanotti (2009) observed that the treatments significantly reduced the understory height, breaking the vertical continuity of fuels.

Since Aleppo pine forests conform a highly inter-connected matrix in the study area, both a disruptive effect on fuel continuity and a significant reduction of understory fuel loads would be highly beneficial in relation to fire risk control at stand and landscape levels. The risk of high intensity surface fires, in particular, would decrease (Fernandes and Botelho, 2003; Duguy et al., 2007a). Low-to-moderate intensity surface fires are characterized by smaller flame lengths that do not overcome easily breaks in vertical fuel continuity. The probability of crown fires (more severe than surface fires) would be, consequently, reduced as well (Pollet and Omi, 2002; Duguy et al., 2007a). The decrease in fine living fuel loads obtained with the studied PB is particularly relevant in relation to fire risk control since fine fuels are highly flammable (Baeza et al., 2002).

Contrarily, dead standing shrub volume and phytomass (of both fine and coarse fractions) strongly increased after the burning, in agreement with other studies (Catalanotti, 2009). Increasing loads of dead standing fuels, particularly the fine fraction, enhance plant combustibility (Baeza et al., 2002; Madrigal et al., 2012), which is one of the components of flammability and more dependent on the dead fraction than on living plant parts (Madrigal et al., 2012).

At the plant community scale, however, the total amount of dead standing fine fuels remained low compared to total living phytomass (the former representing 14% of the latter). Besides, these fuels were not continuously nor homogeneously distributed across the burnt community, but scattered among the green canopies of shrubs that were not affected (or only slightly) by the burning. This spatial distribution likely reduced the potential negative effect that these fuels might have on the fire-proneness of the post-burning understory community. Moreover, our methodology probably led to an overestimation of these dead fuels since it was based on volume-phytomass allometric equations established for living individuals (Duguy et al., 2015). Some parts of living plants, however, are actually not present, or heavily reduced, in dead individuals.

Nevertheless, it appears that the promotion of dead standing fuels may be a concern when applying prescribed burnings in ecosystems dominated by shrubs since the behavior of future fires could strongly depend on the proportion and dynamics of such dead biomass in the fuel complex (Baeza et al., 2002; Duguy et al., 2007a).

In terms of frequency and height reductions caused by the burning, *P. lentiscus* was the least affected shrub species. It was also the one reaching the largest height values in (C) plots. Contrarily, *R. officinalis* and *U. parviflorus*, which reached the second and third largest mean height values, respectively, were strongly affected. These results suggest that total height was not the only structural variable determining the different burning impacts observed among species. Plant flammability is indeed related to several morphological traits; the canopy architecture and the distribution of fuel elements, in particular (Baeza et al., 2011; Madrigal et al., 2012). These traits, which differ between species (Papió and Trabaud, 1991; Duguy et al., 2015), are therefore relevant to fire behavior at the community level (Fernandes and Cruz, 2012; Castagneri et al., 2013).

Higher dead branch proportions are observed for seeder species as compared to resprouters in Mediterranean ecosystems (Saura-Mas et al., 2010; Baeza and Santana, 2015) and retention of standing dead fuel in the lower to mid-canopy is a common feature in seeder shrubs such as *U. parviflorus*, especially in mature (from 9 years onward) and senescent populations (Baeza et al., 2011; Fernandes and Cruz, 2012). In our Control plots, no vegetation treatment had been applied after a

clearing carried out in 1998. Thus, when the studied PB was executed, many *U. parviflorus* adult individuals had reached the maturity stage and the oldest ones might be 15 years old. A high vertical continuity in the distribution of aboveground biomass has been documented for both *U. parviflorus* and *R. officinalis*, as well as a strong concentration of fine fuels in the lower parts of the individuals for the latter species (Fernandes and Pereira, 1993). *P. lentiscus* does not accumulate such large amounts of standing necromass and generally has a very different fuel vertical structure, characterized by a smaller presence of fine living fuels, particularly in the lower parts of the plant. A previous study that we carried out in this plant community confirmed some of these structural differences among our dominant shrubs (Godoy, 2014; Duguy et al., 2015). *P. lentiscus* was characterized by the smallest proportion (52%) of fine aboveground phytomass (estimated as the fine phytomass over total phytomass), whereas *R. officinalis* and *U. parviflorus* reached much larger proportions (70 and 78%, respectively).

Recent studies document that species characteristic of early-successional stages, such as fire-enhanced recruitment seeders (e.g. *Ulex* spp. and *Cistus* spp.), show a marked tendency to retain dead branches in the canopy, while species typical of more advanced successional stages (e.g. *P. lentiscus*) retain less dead biomass loads (Baeza and Santana, 2015). There is still uncertainty about the biological significance of these differences and their relations with the successional niche and the species' post-fire regeneration strategy, though. Besides, we need a more comprehensive understanding of the influence of fuel structural traits on plant flammability and fire behavior at the community level. Our results suggest, nevertheless, that the pre-treatment vegetation heterogeneity (its fine-scale structural heterogeneity, in particular) interacted with the low-to-moderate intensity burning leading to a very heterogeneous burning severity. A high intensity burning would have probably resulted in a much more homogeneous severity.

In synthesis, this study shows that low-to-moderate intensity understory PB may be effective for reducing fire-proneness of *P. halepensis* forests, while promoting their resilience to fire and preserving their diversity. The establishment of appropriate spatial and temporal guidelines for applying PB in these ecosystems requires, however, further knowledge about the effects of factors such as burning intensity, season and frequency on all the ecosystem components (soil, in particular). Excessive burning recurrences could maybe cause a depletion of canopy seed banks and thus constrain natural regeneration of *P. halepensis* populations (Espelta et al., 2008), or lead to cumulative deleterious effects on soil properties (e.g. nutrient concentrations, soil hydrology) that would, in turn, affect plant growth and the whole ecosystem dynamics (Neary et al., 1999; Eugenio and Lloret, 2004; Duguy et al., 2007b; Keesstra et al., 2016).

5. Conclusions

The spring prescribed burning conducted under a *P. halepensis* canopy did not cause short term significant changes in either total species richness, Shannon-Wiener's diversity, or the floristic composition of the understory plant community. The Nanophanerophytes richness did decrease significantly, however, reflecting the reduction of seeder shrubs richness. The frequencies of these latter species, of *Ulex parviflorus* particularly, were also strongly reduced, contrarily to resprouters'. These changes likely resulted in the increase of resprouters' abundance (i.e. cover) in relation to seeders', thus promoting the resilience of the plant community in relation to fire.

The treatment led to the disruption of vertical and horizontal fuel continuities and the strong reduction of understory fuel loads. The post-burning plant community corresponded, thus, to a less fire-prone fuel complex in spite of larger dead standing fuel loads.

Understory prescribed burning appears to be a technique that should be taken into account when designing adaptive forest management strategies in fire-prone Mediterranean landscapes. Further studies

about its medium-to-long term effects on ecosystems properties are required, though.

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